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OBSERVATIONS ON THE SEXUAL CYCLE OF THE GUINEA PIG.

O. ISHII,

PATHOLOGICAL LABORATORY OF THE WESTERN PENNSYLVANIA HOSPITAL,
PITTSBURGH, PA.

In the following work, which was undertaken at the suggestion of Professor Leo Loeb, my aim has been to correlate the microscopical and experimental analysis of the sexual cycle which this author had previously made and further studies which he had planned at that time with a careful study of the cyclic changes as far as they are accessible to the naked eye. These observations were made at the breeding establishment of Miss A. E. C. Lathrop, in Granby, Mass., during the years 1913 and 1914.¹

THE THREE STAGES OF MENSTRUATION AND HEAT.

1. *Præstrum*.—This period continues for one to one and a half days, during which time the external genital organs become congested and swollen and a slight serous secretion is noticeable. This secretion, while in some instances turbid or viscid, is in the majority of cases more or less transparent; while, as before said, this period averages one to one and a half days, in some instances it may continue for two or three days or more. In the last 4 or 5 hours toward the end of this period a maximum in these changes is reached. This is followed by the period of heat. The duration of the proœstrus period is indicated on the following table. Ninety-four (94) animals served for this observation.

	Length of Proœstrus Period.					
	½ Day.	1 Day.	1½ Day	2 Days.	3 Days.	4 Days.
No. of guinea pigs.....	1	39	34	11	8	1

¹ Accidental conditions greatly delayed the publication of this paper. In the meantime there has appeared a study of Stockard and Papanicolaou on the œstrous cycle of the guinea pig. Notwithstanding this long delay in publication, we believe that our observations present new facts of interest and are worth recording.

On the basis of these observations it may be reasonably said that the average length of this period in an animal of normal physical condition is from one to one and a half day, but after puerperium, or in case of weakness or of pathologic conditions, a shortening or prolongation may be brought about.

2. *Œstrus, or Heat*.—The approach of this period is made apparent by excessive menstrual secretion during the last 4 or 5 hours of proœstrum. This continues for 6 or 7 hours of the œstrus period. This is followed by the secretion of a small quantity of moisture which may be just noticeable, or during the last 3 or 4 hours of the œstrus period menstrual secretion may be lacking altogether; still heat is present in this period.

I give the following data as to the length of period of heat:

	Length of Heat Period.				
	5 to 6 Hrs.	7 to 8 Hrs.	9 to 10 Hrs.	11 to 12 Hrs.	13 to 14 Hrs.
No. of guinea pigs	6	51	62	30	9

As can be seen from the above figures, from 8 to 11 hours is the average length of the heat period in the healthy animal. I found those guinea pigs in which the periods were longer (12 to 14 hours) or shorter (5 to 6 hours) to have been lacking in vigor or to have shown abnormal physical conditions. In the normal animal I feel justified in claiming, on the average, 9 to 11 hours as the correct length of this period in the normal guinea pig.

3. *Metœstrum*.—This is the period following the œstrus period and might be considered as the period of recovery from the œstrous changes. The length of this period depends almost wholly on the condition of the animal. In the normal animal $2\frac{1}{2}$ to 3 days are required until the normal condition is re-established. From the figures that follow it will be noticed that the length of this period varies from $1\frac{1}{2}$ to 5 days, but my observations have convinced me that where the recovery is shorter or longer than the average period, the animal is not in a normal healthy condition.

	Length of Metœstrus Period.							
	$1\frac{1}{2}$ Days.	2 Days.	$2\frac{1}{2}$ Days.	3 Days.	$3\frac{1}{2}$ Days.	4 Days.	$4\frac{1}{2}$ Days.	5 Days.
No. of guinea pigs . . .	4	9	30	20	15	10	5	4

I may state that at this period a slightly transparent serous or a turbid or viscid secretion can be noticed; but within 2 or 3 days this will disappear, and the swelling of the external organ will cease and normal conditions will again prevail.

PHENOMENA OF FIRST MENSTRUATION OR HEAT PERIOD IN THE GUINEA PIG.

The first heat or menstruation of the guinea pig differs in some respects from the later periods of heat. The symptoms of proœstrum are of much longer duration. While as stated above, the normal proœstrum lasts about 1 to 1½ days, during the first menstruation a slight secretion and swelling continues for 3 to 8 days; only then appears the period of heat proper. In some instances the secretion and swelling disappear temporarily. Then a few days later it begins again and now develops into the regular heat. As stated, generally the duration of the proœstrum is variable and usually longer in the first menstrual period.

DIÆSTRUS PERIOD OF THE GUINEA PIG.

The diœstrus period is the length of time between two consecutive menstruations or heat periods. Through observation of the condition of heat we determined the length of the sexual cycle in the guinea pig; we used for this purpose a considerably larger material than Loeb¹ and Stockard and Papanicolaou² used in their observations. While our average agrees with that of the aforementioned authors, we found a greater range of variation than Stockard and Papanicolaou. From the observations of Loeb it follows that in some exceptional cases the period may be even shorter than that found by us.

	Length of Time Between Heat.							
	14½ Days.	15 Days.	15½ Days.	16 Days.	16½ Days.	17 Days.	17½ Days.	18 Days.
No. of guinea pigs. . . .	1	40	72	62	36	12	8	1

From these figures we may conclude that the average duration of this period was 15 to 16½ days. I found that where the length of time was decidedly shorter (14½ days) or longer (17 to

¹ Leo Loeb, BIOLOGICAL BULLETIN, 1914, XXVII., 1.

² C. R. Stockard and G. Papanicolaou, *Am. Jour. Anat.*, 1917, XXII., 225.

18 days) than the average, the animals were either in a weak or pathological condition, and that menstrual irregularities subsequently followed. My continuous experiments made on this subject covered both winter and summer of 1913, and the winter of 1914 in Granby, Mass., and during all these seasons, through all temperatures, the same condition prevailed.

GENERAL PHENOMENA OF MENSTRUATION AND HEAT AND PREGNANCY.

Physical Phenomena of Menstrual Period.

One of the foremost indications of the approach of the period of menstruation or heat is the physical change noticed in the animal. The muscles and joints become tender and relaxed, and by this change it can be determined, whether the animal is normal and healthy. During this period nervousness and a certain mental depression are noticeable; and when the period is over the symptoms most apparent indicate fatigue or exhaustion. However, by the end of the second or third day this fatigue has entirely disappeared and within $1\frac{1}{2}$ to 2 days after cessation of heat a normal animal has regained its full vitality.

Relation between Menstruation and Falling Out of Hair.

I have found, particularly in the guinea pig, rat and rabbit an additional visible sign of heat, viz., the falling out of the hair in unusual quantities during the period of menstruation; as a result of this happening, the external appearance of the animal becomes somewhat glossy. We can determine this by comparing the ease with which the hair can be made to fall off by rubbing the skin in the menstruating animal, on the one hand, and in the infantile, pregnant, amœstrous female or male, on the other hand. In exceptional cases a slight menstrual secretion may develop during pregnancy; in this case the falling out of the hair is slight in accordance with the slight degree of menstrual activity.

Specific Odor of Females during the Period of Heat.

Many (but not all) males can evidently clearly distinguish between females which are in the period of heat on the one hand and those in which there is merely menstrual secretion and in

which both are lacking on the other hand. Therefore the male attempts copulation only in the former case. When a number of animals of both sexes are together and among them is a female in the heat period, the males run around and search for that particular female, ultimately finding it.

I am convinced from this searching of the male for the female in heat that he is led to do so by a special odor characteristic of the female, when it reaches the heat period. This peculiarity is common to the mouse, the rat and the rabbit.

Influence of Food upon the Character of Heat and on the Time when Sexual Maturity is Reached.

The vigor of the heat in guinea pigs depends upon the nourishment which the animals have received. Guinea pigs which had been poorly fed develop weak heat. This applies to the duration of the heat as well as to the vigor of the symptoms. The length of the diœstral period does on the other hand not seem to be affected by the state of nourishment.

I made observations on the influence of food on the time when sexual maturity is reached.

I. On especially prepared rich food the first heat was observed 45 to 60 days after birth.

II. On usual food 55 to 70 days after birth.

III. On food of poor quality 75 to 100 days after birth.

The usual food consisted of hay (or grass), carrots (or beets) and oats. In the rich diet corn cake was added, while the poor diet consisted merely of hay (or green grass) and oats. When the quality of the food was above the ordinary, its effect on the size of the guinea pig as well as their physical condition in other respects could be seen. They were of the average condition, when ordinary food was given at regular intervals, and the poorly fed animals were poorly developed physically. The food is therefore of the greatest importance as far as the time of sexual maturity and the character of the heat are concerned.

Influence of Climate on the Character of the Heat and the Length of Sexual Cycle in the Guinea Pig.

The extreme temperature of the summer months (a temperature of over 90° F. in Granby, Mass.) has a weakening effect on

the guinea pigs. And the heat is therefore not so vigorous as it would be under other climatic conditions. The length of the diestrous period on the other hand seemed to be the same during the warm and cold season of the year.

Does Contact with the Male Influence the Time of Appearance of the First Heat?

If young female guinea pigs are kept in a cage with males and other guinea pigs of the same descent are kept separated from males, the first heat appears in both lots at the same age. This shows that psychical factors such as the stimulation of the male does not influence those conditions which lead to the first heat.

The Copulation-reflex of the Heat Period and the Diagnosis of the Heat Energy.

This reflex can be elicited by the male guinea pig seeking copulation, when it touches or gently massages with his forefeet the lumbar portion of the spinal column of the female which is in heat. The female will then lift up the tail and the vagina will be opened in preparation of the copulation. The same reflex can be called forth if an observer touches with his finger the same part of the body of the female guinea pig. The readiness and vigor with which the reflex occurs can serve as a measure of the energy or vigor of the heat.

Menstruation during Pregnancy.

I very carefully watched twenty guinea pigs during their state of pregnancy for a sign of menstruation and found in ten no evidence of menstrual secretion, but in the remaining ten there was some secretion present; not all of those however showed signs of heat. The menstrual period is not definite during pregnancy. Statistically my results were as follows:

Menstruation was noticed in 3 guinea pigs 27 days after copulation

"	"	"	"	3	"	"	30	"	"	"
"	"	"	"	2	"	"	40	"	"	"

2 " " had menstrual secretion twice, the first time 15 days and the second time 30 days after copulation.

While in these cases the swelling of the external genitalia and the secretions are manifest, they are slight. The secreted material

is mostly transparent, but sometimes turbid. It continued for 3 to 8 days in my observation; then the external genitalia returned to a normal condition.

Some authors suppose that the diagnosis of the menstrual secretion is very difficult in the guinea pig; however careful observation has shown me that the diagnosis can be readily made and hardly misinterpreted.

Diagnosis of Pregnancy about 14 to 15 Days after Copulation.

About 14 or 15 days after copulation we can correctly determine the success or failure of the impregnation. If at that time the external genitalia are in a normal condition we may almost always assume a successful pregnancy. If, on the other hand, there should be within that time a noticeable swelling of the external genitalia, accompanied by secretion, this may in all cases be taken as an indication of failure. As we have stated above, the same phenomenon may be present, perhaps in a milder form, at this period of pregnancy, but this is a very rare occurrence; and as a general rule in the case of failure (early abortion) the secretion and swelling is much more marked.

The Sexual Cycle in Cases of Early Abortion.

In cases of early abortion I found the period of heat in some cases somewhat accelerated and more irregular than in normal animals.

DIOESTRUM.

	Length of Heat Following Copulation.				
	12½ Days.	13½ Days.	14½ Days.	15½ Days.	16 Days.
No. of guinea pigs examined	1	2	2	3	5

As shown in the table, the heat period may appear as early as 12½ or 13½ days after copulation. In control cases the shortest period observed was 14½ days and this occurred only once; and, as I stated above, I believe that in normal cases 15 days represents the minimum and that the shorter periods are usually found in cases of abortion.

The Length of the Period of Gestation in the Guinea Pig.

On the basis of our observations we can give the following statistical data concerning the length of the period of pregnancy in the guinea pig.

	Length of Gestation Period.							
	61 Days.	62 Days.	64 Days.	66 Days.	67½ Days.	68 Days.	69 Days.	71 Days.
No. of pregnant guinea pigs	2	2	4	4	8	15	5	1

The shortest period was 61 days; but those young animals which are born 61, 62 and 64 days following copulation show a certain lack of development; they are really born prematurely and in the majority of cases they soon die, although they may be able to survive. Those born 66 days after copulation usually lived and continued to grow, but those born from 67 to 69 days following copulation show the maximal development after birth; these have the best chance to develop into absolutely healthy, perfect animals. We may therefore conclude that 68 days is the regular period of gestation in the guinea pig.

Separation of the Symphysis Pubis in the Guinea Pig at the End of Pregnancy, at the Time of Birth and During the Period Directly Following Birth.

Through examination with the finger we discern in the guinea pig a gradual separation of the symphysis pubis which begins about 61 to 63 days after copulation and increases as the time of labor approaches to a width of 7 to 8 millimeters or more; but within one or one and a half days after birth the symphysis pubis assumes again its normal condition. The following table shows the time when the separation becomes apparent:

	Beginning Separation of Symphysis Pubis.		
	61 Days, Following Copulation.	62 Days, Following Copulation.	63 Days, Following Copulation.
No. of pregnant guinea pigs.	5	5	4

The length of time from the beginning of the separation of the symphysis to the onset of labor is shown on the following table:

	Duration of Period of Separation of Symphysis Pubis Prior to Birth.		
	4½ Days.	5 Days.	7 Days.
No. of pregnant guinea pigs.....	1	6	7

The following table shows the length of time necessary for the symphysis pubis to return to its normal condition following labor:

	Time when the Symphysis Pubis has again Become Normal Following Labor.			
	½ Day.	1 Day.	1½ Days.	2½ Days.
No. of guinea pigs.....	4	8	5	1

From these data we may conclude that the separation of the symphysis pubis begins from 5 to 7 days previous to birth, or from the 61st to the 63d day after copulation. Under ordinary conditions birth should not take place before the 5th day following this separation. The length of the period of gestation should therefore usually be 68 days.

Preparation for Labor.

In the guinea pig the separation of the symphysis pubis serves as a preparation for parturition, inasmuch as the orifice of the normal pelvis is too narrow to permit birth to take place. Moreover we find at the same time the same remarkable softness and elasticity of the muscles and joints as during the ordinary menstrual period. This same effect (emanating from the ovary or pituitary gland) I have also noticed in the rat and in the rabbit and I presume it is the same in all mammals.

The Time of the First Heat in the Puerperium.

The time of the beginning of heat in the period directly following labor is somewhat variable. In 20 guinea pigs in which parturition set in at the normal time (67 to 69 days after copulation) I found the following figures:

	Beginning Puerperal Heat After Parturition.				
	Soon After	3 Hours After.	5 Hours After.	7 Hours After.	No Heat.
No. of examined guinea pigs	7	7	3	1	2

As our table shows, in 2 out of 20 guinea pigs no heat at all was observed at this period. There was evidence pointing to the conclusion that the heat is less vigorous at this stage than in the normal menstrual period. On the other hand the heat seems perhaps to be of a somewhat longer duration at this period as shown in the following table:

	Duration of Puerperal Heat.		
	7 to 9 Hrs.	10 to 11 Hrs.	12 to 13 Hrs.
No. of guinea pigs.....	8	7	7

We find therefore that in about one third of the guinea pigs at this period the average duration of heat was 12 to 13 hours, while in normal animals the heat continues for that length of time only in a small minority of cases. Whether or not heat occurs in the period directly following parturition depends upon the duration of the period of gestation as shown in the following table:

	Duration of Pregnancy.						
	61 Days.	62 Days.	64 Days.	66 Days.	67½ Days.	68 Days.	69 Days. 71 Days.
No. of observed guinea pigs.	2	2	4	4	8	15	5
Puerperal heat.....	-2	-2	-4	-1/+3	-1/+7	-2/+13	+5/+1

+ coming in heat; - not in heat.

This table shows that heat does not occur in the period directly following parturition in cases in which the duration of pregnancy was less than 66 or 67 days. In cases in which the duration of pregnancy was less, birth occurred prematurely and the phenomena of the puerperium had not yet fully developed at the time of the completion of labor. If in cases of parturition occurring 61 or 62 days after copulation the first heat following parturition would take place 6 or 8 days later, the first heat would correspond to a typical puerperal heat, provided the duration of pregnancy would have been 68 or 69 instead of 61 days.

On the Duration of the Sexual Cycle following Parturition.

The time of the second menstruation in the period following parturition is rather variable as shown in the following table:

	Development of Second Menstruation Following Parturition.									
	15½ Days.	16 Days.	16½ Days.	17 Days.	17½ Days.	18 Days.	21 Days.	22 Days.	23 Days.	Total.
No. of guinea pigs	2	1	4	5	2	3	1	1	1	20

Among 20 guinea pigs in the period following the puerperium I found complete menstruation and heat in 15 cases, while in 5 animals I found only menstrual secretion without heat. The majority of these animals suckled their young and among those the deviation from normal was somewhat less; in these cases the duration was mostly 15½ to 18 days.

Effect of Lactation and Non-Lactation on the Periodicity of the Sexual Cycle after Parturition.

In cases in which the young were suckled the next period of heat took place approximately at the normal time and the conditions continued from then on in a normal manner. It was different in cases in which bodily weakness of the mother prevented the suckling of the young. In the latter cases the return of menstruation was delayed so that it occurred as late as 21 to 23 days after parturition. In the normal suckling animal the sexual periodicity following labor is therefore similar to that of the normal animal, although certain minor variations depending on the vitality of the animal occur even in such cases. The second or third menstruations occur usually after the regular interval of 15 to 16 days even in the weak animal. In the latter, however, we may at these times instead of heat merely find menstrual secretion.

The Effect of Suckling on the Mother and the Young.

Marshall¹ expresses the opinion that in the young separated prematurely from the mother growth will continue. My own observations lead me to a different conclusion. I have found

¹ F. H. A. Marshall, "The Physiology of Reproduction." London, 1910.

that if a mother suckled three young, the growth of the latter was very slow, or death resulted; in addition the weakening effect on the mother was quite noticeable; it sometimes caused her death, and in most cases the death of the young occurred. If the young died, the mother soon regained her health and strength. The result will therefore be disappointing either as far as the condition of the mother or of the young is concerned. It has been my experience that when the young were taken away from the mother within 15 or 20 days after birth and the ordinary vegetable and oat diet was given them, development was very slow and in most cases death occurred. In any case the young to attain healthy growth should not be taken from the mother until more than 25 to 30 days of age. Under natural conditions they cease suckling after 35 to 40 days, when they seek their own food. I am therefore of the opinion that a litter of three very seldom shows normal development when suckled by one mother.

When I combined one mother with two and another with three young, each mother suckled on the average $2\frac{1}{2}$ young. In such cases I obtained good results. While two or three young is the average size of a litter, I have known the number to vary from one to six; the latter number, however, only occurred once in my observation. When but one young is born, it is usually well developed and vigorous; but to be successfully raised it must be suckled for the usual period or at least for a time approaching it. There is another symptom in addition to the bodily weakness, which the mother shows as the result of too intensive suckling: it consists in the changing of the color of the pupil of the eye which becomes pale or white. It may be associated with general exhaustion.

Under what Condition is Copulation followed by Pregnancy?

As we stated above the normal duration of heat is about 10 hours. If copulation took place within 3 or 4 hours after the beginning of heat, pregnancy followed only rarely. If the copulation took place at a later period of the heat, better results were obtained. According to my observations pregnancy occurred in about 73 per cent. to 80 per cent. of the cases. In such cases in which copulation was not followed by pregnancy a second or

third attempt during the next two periods of heat were mostly successful.

Sobotta¹ states that the guinea pig in captivity can become pregnant more frequently in summer than in winter. My observations do not bear out this statement. In my experience the pregnancies resulted almost as often in the cold as in the hot season. The winter climate is better adapted for the guinea pig in captivity than the hot summer weather when the temperature is liable to exceed 90° F. Under those conditions the animal suffers and becomes poorly developed as the result of undernourishment. On the other hand, it is almost always in good condition in winter. Therefore the cold season agrees better with guinea pigs than the hot season under conditions of captivity. In exceptional cases the guinea pig may become in winter time too fat to be favorable for impregnation; and this may even happen in summer time.

Relation between Growth, the First Period of Heat and the Period of Sexual Maturity in the Guinea Pig.

In my observations the weight of the guinea pig is ordinarily three ounces soon after birth. However, the weight of the young is in accordance with the age of the mother and also the number of the litter. As a rule the young born from a young mother are small in size and in litter. On the other hand, when the mother is older than 5 months, the weight of the young is mostly larger. For instance, in one litter the young weighed 6 or 7 ounces soon after birth.

Minot² has concluded that the guinea pig is slow in growing and that it attains its full size one year after birth. My observations are as follows: The young guinea pig at the time of the first heat was about two months old; about 7 to 10 days before the beginning of heat, the growth almost stopped or at least progressed very slowly. At the time of the first heat period the average weight was 11 to 13 ounces. After the first heat period had passed it began to grow very rapidly. About two or three

¹ Sobotta, *Anat. Hefte*, 1906, XXXII.

² Minot, C. S., "Growth and Senescence," *Journ. Physiol.*, 1891, XII., 97. "Problems of Age, Growth and Death," *Popular Science Monthly*, 1907, LXX., 481, and LXXI., 97 and succeeding numbers.

months later, at the age of 4 to 5 months, it attained its full weight, about 20 to 28 ounces, but one exceptional animal weighed 34 ounces in a non-pregnant condition. However, if we feed a special diet of nutrient material and the animal is otherwise well taken care of, then the growth progresses rapidly and the heat begins earlier than usual. The guinea pig which weighed 34 ounces was fed on the usual farm or laboratory food. Therefore we must remember that the growth of the young depends considerably upon the character of the food.